

Dietary Overlap of Swift Foxes and Coyotes in Northwestern Texas

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ABSTRACT.—Predation by coyotes (*Canis latrans*) has been documented as the main cause of mortality in most populations of swift foxes (*Vulpes velox*), although reasons for such high predation rates were often unclear. Additionally, coyotes kill but generally do not consume swift foxes, suggesting coyotes kill for reasons other than food. To better understand ecological relationships between these species, we studied dietary overlap of syntopic coyotes and swift foxes in northwestern Texas from 1998 to 2000. Both species consumed the same food items and had similar seasonal changes in diets, although the order of these items differed for each species. Overall, coyotes and swift foxes had high dietary overlap ($R_o = 0.856$), although some dietary partitioning was evident based on food size categories. Dietary overlap was least in summer ($R_o = 0.714$) and greatest in winter ($R_o = 0.859$). Swift fox diets were dominated by small food items (*i.e.*, rodents and insects), whereas coyote diets had nearly equal representation of all food classes. The similarity in diets between coyotes and swift foxes indicated the potential for resource competition between these species, although we did not determine food availability. Regardless, the killing and spatial displacement of swift foxes by coyotes throughout their distribution might be due to their high food resource overlap, especially because coyote populations tend to be limited by prey availability.

INTRODUCTION

The greatest cause of mortality documented for swift foxes throughout their distribution was predation by coyotes (Covell, 1992; Carbyn *et al.*, 1994; Sovada *et al.*, 1998; Kitchen *et al.*, 1999; Olsen and Lindzey, 2002; Harrison, 2003; Kamler *et al.*, 2003a). Coyotes kill, but generally do not consume swift foxes (Kitchen *et al.*, 1999; Matlack *et al.*, 2000; Kamler *et al.*, 2003a), suggesting killing is for reasons other than food. Additionally, coyotes can spatially displace swift foxes, thereby suppressing local fox numbers (Kamler *et al.*, 2003b). Predation of smaller canids by coyotes also has been documented in kit foxes (*Vulpes macrotis*) (Cypher and Spencer, 1998; Ralls and White, 1995), red foxes (*V. vulpes*) (Sargeant and Allen, 1989) and grey foxes (*Urocyon cinereoargenteus*) (Fedriani *et al.*, 2000), and coyotes reportedly displaced red foxes as well (Voigt and Earle, 1983; Harrison *et al.*, 1989). Interspecific killing is common among mammalian carnivores, and can result in relatively high mortalities and population suppression (Palomares and Caro, 1999). Additionally, interspecific killing is

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more common within taxonomic families of carnivores, due to closely related species being constrained by similar ecological needs (Donadio and Buskirk, 2006) and appears to be particularly common within canid communities in North America (Peterson, 1995; Ballard *et al.*, 2003).

Reasons for such high rates of killing swift foxes by coyotes is unclear, but might be the result of competition for limited resources (Scott-Brown *et al.*, 1987; White *et al.*, 1995; Cypher and Spencer, 1998). In theory, interference competition, including interspecific killing (where the victim is not consumed), could free up food resources that would be consumed by the victim (Case and Gilpin, 1974; Polis *et al.*, 1989; Palomares and Caro, 1999). Thus, although interference competition is inferred between coyotes and swift foxes due to high kill rates and spatial displacement, little is known about their potential competition for the same resources. Dietary overlap between two species can reflect the potential for competition for those resources (Schoener, 1983). However, for competition to occur those food resources must be limited, which often is difficult to determine.

Coyotes are limited by numbers of their major prey in many regions of their distribution (Knowlton and Stoddart, 1983; Knowlton and Gese, 1995), at least in areas with little human persecution. For example, coyote numbers were positively related to numbers of snowshoe hares (*Lepus americanus*) in Canada (Todd *et al.*, 1981; Todd and Keith, 1983), black-tailed jackrabbits (*L. californicus*) in Utah (Clark, 1972; Gross *et al.*, 1974; Mills and Knowlton, 1991) and Idaho (MacCracken and Hansen, 1987) and rabbits (*Sylvilagus* sp.) and arvicolines (*Microtus* sp.) in Kansas (Gier, 1968), indicating coyote numbers were limited by prey availability. Thus, if syntopic (*i.e.*, species sharing same habitat within their geographic ranges) coyotes and swift foxes consume similar prey species, then there is high potential for food competition between these two species. Despite this potential competition, dietary overlap between syntopic swift foxes and coyotes has been little researched, and was examined only in one previous study (Kitchen *et al.*, 1999).

The purpose of this paper was to determine the extent of seasonal and annual dietary overlap between swift foxes and coyotes in northwestern Texas. Because coyotes had a severe negative impact on swift foxes on our study site (Kamler *et al.*, 2003a,b), comparing dietary overlap could help elucidate why coyotes killed and spatially displaced swift foxes on this site.

METHODS

Study area.—Research was conducted in Dallam and Sherman counties in northwestern Texas (36°24–31'N, 102°19–64'W). Habitat on our study site was dominated by native short-grass prairie, and included continuous native prairie on Rita Blanca National Grasslands (Dallam County), as well as fragmented prairie on the Dallam and Sherman county border. Short-grass prairie vegetation consisted primarily of blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) that was moderately to heavily grazed by cattle. Although parts of the study site was interspersed with additional habitat types, including agricultural fields and Conservation Reserve Program (CRP) fields, nearly all feces (>95%) were collected in native prairie, thus feces from all areas were pooled for the purposes of this paper.

Feces analysis.—Dietary overlap and diversity between swift foxes and coyotes were determined by analyses of feces (Lemons, 2001). Feces were collected from August 1998 to December 2000 during four seasons defined as summer (July–September), autumn (October–December), winter (January–March), and spring (April–June). Eight 2-km transects were walked once during each season. Although transects were not always cleared

prior to collection, feces were collected in the middle or last month of each season, to help ensure that feces were from that season. A minimum of 20 feces per species were collected during each season. Feces also were collected at den sites, and opportunistically in some seasons, to achieve minimum sample size. Feces were identified to species according to size and shape (Murie, 1974). Each feces was individually bagged and labeled with date, season, species, location, and habitat type.

Following collection, feces were placed in nylon mesh bags and soaked in warm water with detergent for 30 min in an automatic washing machine. Following soaking, bags were washed for two cycles and allowed to air dry. After bags dried, they were opened and food remains identified (Lemons, 2001). Reference collections and keys for teeth and hairs were used for identification of prey remains (Gilbert, 1990; Moore *et al.*, 1997).

Percent volume of food items per feces (percent volume) and percentage of feces containing a specific food item (frequency of occurrence) were used to assess differences in diets. To minimize bias associated with over-estimation of small mammals in diets of carnivores, food items were placed into one of three categories (*i.e.*, major, minor and trace) as outlined by Knowlton (1964). Items comprising >40% of a feces were recorded as major items, those 5%–39% were recorded as minor items, and those <5% were recorded as trace. Trace items were excluded from analyses to minimize bias (Knowlton, 1964).

Food items were identified and separated into 1 of 5 taxonomic categories (*i.e.*, insects, mammals, birds, crops and vegetation). Mammalian food items were identified to genus and grouped into one of four categories based on size; small rodents (body mass < 100 g), large rodents (body mass > 100 g), lagomorphs and ungulates (Lemons, 2001). Comparisons of percent volume of food items between years and among seasons within both taxonomic categories and food size categories were conducted by use of chi-square contingency tables (Sokal and Rohlf, 1999). A coyote reduction program, conducted by personnel from the U.S. Department of Agriculture, occurred on the western half of our study site during 2000. When feces from only the western half of the study site were analyzed separately, no significant differences were found in diets of swift foxes before and during coyote reduction (Lemons, 2001), thus data from both parts of the study site were pooled in subsequent analyses.

Dietary diversity was determined for swift foxes and coyotes by year and season with Shannon-Weiner diversity indices (Shannon, 1948). Frequency-of-occurrence calculations were used in determining diversity indices. Student's *t*-test was used to test for differences between diversity of coyote and swift fox diets among seasons and between years (Zar, 1999). Horn's Index was calculated to determine degree of overlap between swift fox and coyote diets (Horn, 1966).

RESULTS

From August 1998 to December 2000, 534 swift fox and 482 coyote feces were collected. Twenty-six taxonomic groups of food remains were identified including insects, lagomorphs (*Lepus californicus* and *Sylvilagus* sp.), rodents, cattle, pronghorn (*Antilocapra americana*), reptiles (*i.e.*, snake and lizard species), birds, crop seed (*i.e.*, corn, wheat, sorghum and sunflower seed) and vegetation (*i.e.*, grass and forbs; Lemons, 2001). Small rodents identified in feces included kangaroo rats (*Dipodomys ordii*), pocket mice (*Perognathus* sp. and *Chaetodipus* sp.), deer and/or white-footed mice (*Peromyscus* sp.), harvest mice (*Reithrodontomys* sp.), grasshopper mice (*Onychomys ochragaster*) and voles (*Microtus* sp.; Lemons, 2001). Large rodents identified in feces included black-tailed prairie dogs (*Cynomys ludovicianus*), woodrats (*Neotoma* sp.), hispid cottonrats (*Sigmodon hispidus*), pocket gophers (*Cratogeomys* sp.) and ground squirrels (*Spermophilus* sp.; Lemons, 2001).

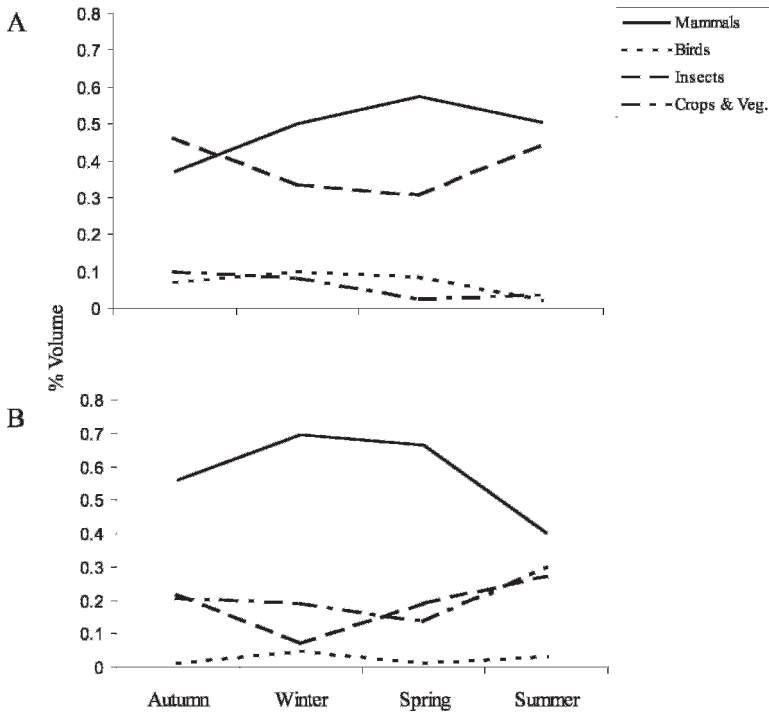


FIG. 1.—Percent volume of foods, based on taxonomic categories, in diets of swift foxes (*Vulpes velox*; A) and coyotes (*Canis latrans*; B) from northwestern Texas, August 1998–December 2000

Diets differed by season both for swift foxes ($\chi^2 = 25.2$, $df = 12$, $P = 0.014$) and coyotes ($\chi^2 = 45.2$, $df = 12$, $P < 0.001$), but not across years (swift fox: $\chi^2 = 8.2$, $df = 4$, $P = 0.086$; coyote: $\chi^2 = 4.7$, $df = 4$, $P = 0.314$) when testing taxonomic categories (*i.e.*, insects, mammals, birds, crops and vegetation). For swift foxes, mammals were the main taxonomic group in their diet in all seasons except autumn, when insects dominated (Fig. 1). For coyotes, mammals were the main taxonomic group in their diet during all seasons (Fig. 1).

Food size categories (*i.e.*, insects, small rodents, large rodents, lagomorphs and ungulates) in diets of swift foxes and coyotes differed during both years (1999: $\chi^2 = 84.2$, $df = 4$, $P < 0.001$; 2000: $\chi^2 = 67.5$, $df = 4$, $P < 0.001$) and across seasons (autumn: $\chi^2 = 65.9$, $df = 4$, $P < 0.001$; winter: $\chi^2 = 61.8$, $df = 4$, $P < 0.001$; spring: $\chi^2 = 29.1$, $df = 4$, $P < 0.001$; summer: $\chi^2 = 27.3$, $df = 4$, $P < 0.001$). Insects and small rodents dominated the diets of swift foxes in all seasons (Fig. 2), whereas coyote diets had a more equal representation of all food size categories (Fig. 2). For both swift foxes and coyotes, small rodents were the main prey items in most seasons, whereas proportion of insects varied throughout the year (Fig. 2).

Dietary diversity was high for both species, but coyotes had a more diverse diet than swift foxes overall and during each year (Table 1). Diversity differences were greatest in summer and autumn, whereas they did not significantly differ in winter or spring (Table 1). High indices of dietary overlap occurred during all seasons and years for both species (Table 1). Dietary overlap was greatest in winter and least in summer (Table 1).

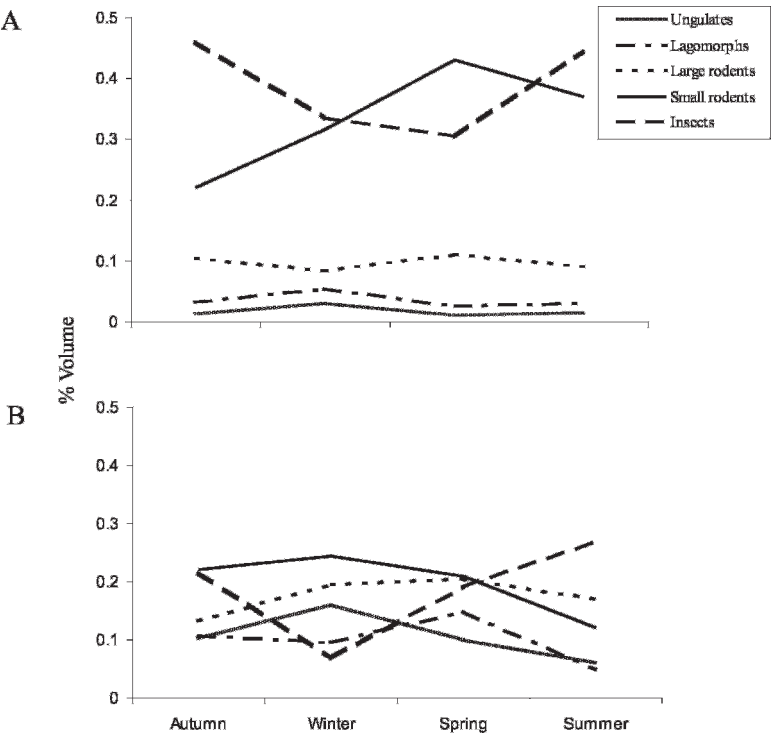


FIG. 2.—Percent volume of food-size categories in diets of swift foxes (*Vulpes velox*; A) and coyotes (*Canis latrans*; B) from northwestern Texas, August 1998–December 2000

DISCUSSION

Swift foxes and coyotes exhibited relatively similar changes in diets corresponding with seasonal changes, which likely resulted from the generalist and opportunistic feeding behavior of both species. Previous studies reported that changes in food availability associated with seasonal changes impacted composition of coyote diets, indicating coyotes were highly opportunistic feeders (Gipson, 1974; Bowyer *et al.*, 1983; Andelt *et al.*, 1987;

TABLE 1.—Seasonal, annual and overall dietary diversity (Shannon 1948) and overlap (Horn 1966) for swift foxes (*Vulpes velox*) and coyotes (*Canis latrans*) in northwestern Texas, August 1998–December 2000

Period	Shannon Diversity Index			Horn's Index
	Swift Fox	Coyote	P-value	
Spring	3.203	3.574	0.401	0.733
Summer	2.760	3.634	0.032	0.714
Autumn	2.929	3.743	0.034	0.822
Winter	3.281	4.000	0.086	0.859
1999	3.338	3.885	0.012	0.804
2000	3.166	3.885	0.003	0.835
Overall	3.135	3.941	0.006	0.856

Kamler *et al.*, 2002). Similarly, swift foxes were shown to be opportunistic feeders, therefore seasonal changes in food availability likely impacted diet composition of swift foxes (Kilgore, 1969; Scott-Brown *et al.*, 1987; Kitchen *et al.*, 1999; Sovada *et al.*, 2001). For swift foxes and coyotes in our study, consumption of insects peaked in summer and autumn, whereas consumption of mammals peaked in winter and spring, which likely reflected the changing abundance of these food items throughout the year. In most seasons, mammals were more dominant in coyote diets than in swift fox diets.

During all seasons and both years, swift foxes primarily consumed small rodents or insects and did not rely as much on larger food items (*i.e.*, large rodents, lagomorphs and ungulates). Swift foxes may naturally consume small food items, including insects and small rodents, which are more appropriate to their body size and predatory specializations (Lemons, 2001). The relatively low consumption of ungulates throughout the year by swift foxes likely was the result of scavenging, as swift foxes are not known predators of ungulates. In contrast, coyotes consumed larger-sized prey items than swift foxes, which likely reflected their larger body size and corresponding different predatory abilities and energetic needs compared to swift foxes (Kitchen *et al.*, 1999). In general, coyotes often consume larger prey items than syntopic fox species, such as kit (White *et al.*, 1995; Cypher and Spencer, 1998) and red foxes (Green and Flinders, 1981; Major and Sherburne, 1987).

We documented high overlap in the diets of swift foxes and coyotes, which was surprising given their considerable differences in body sizes and predatory abilities. Our results were similar to the only previous study that investigated diets of syntopic swift foxes and coyotes (Kitchen *et al.*, 1999). In that study, both species had an overall dietary overlap ($R_o = 0.835$), ranging from 0.71 to 0.91 in different seasons (Kitchen *et al.*, 1999). Perhaps because prey diversity is relatively low in the western Great Plains, coyotes and swift foxes have such a high degree of dietary overlap. However, our results, as well as those from Kitchen *et al.* (1999), showed that some dietary partitioning between swift fox and coyote was evident when considering the size of mammalian prey items.

The relatively high dietary overlap between swift foxes and coyotes suggested competition for food resources potentially could occur between these species. This might especially be true given that coyote numbers tend to be limited by prey abundance (Clark, 1972; Gross *et al.*, 1974; Todd *et al.*, 1981; Todd and Keith, 1983; MacCracken and Hansen, 1987; Mills and Knowlton, 1991; Knowlton and Stoddart, 1983; Knowlton and Gese, 1995), including coyote populations in the Great Plains (Gier, 1968) and Texas (Windberg, 1995). Thus, any consumption of similar prey species by syntopic swift foxes potentially could reduce limiting food resources for coyotes. Consequently, high dietary overlap might be the reason for high kill rates and spatial displacement of swift foxes by coyotes on our study site, and possibly other areas throughout their distribution.

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